

Relationships between age, growth, diet and environmental parameters for anchovy (*Engraulis encrasicolus* L.) in the Bay of Bénisaf (SW Mediterranean, west Algerian coast)

by

Mahmoud BACHA* (1, 2, 3, 4), Aissa MOALI (4), Nasr-Eddine BENMANSOUR (5),
Jean-Michel BRYLINSKI (1, 2, 3), Kélig MAHÉ (6) & Rachid AMARA (1, 2, 3)

ABSTRACT. - Age, growth and diet of anchovy were studied for the first time from samples collected in the Bay of Benisaf (west Algerian coast) during summer (spawning period) and autumn (recruitment period) 2007. Age structure and growth parameters were determined by otolith (sagitta) analyses. The von Bertalanffy growth function fitted to age-length data showed that most of anchovy growth is achieved during the first year of life, suggesting that this stock is primarily supported by the smallest age groups and has a strong dependence on recruitment. There were no significant differences between males and females, and pooled mean parameters were: $L_{\infty} = 15.61$ cm, $k = 0.75$ per year and $t_0 = -1.32$ years. Whatever the age-class anchovy is strictly zooplanktivorous. Copepods constituted the dominant group (64% O; 81% N), while other crustaceans, mollusc larvae and fish larvae were less represented. The main species of copepods consumed were by order of abundance: *Candacia longimana*, *Oncaea mediterranea* and *Pleuromamma abdominalis*. The results indicated a diversification of the diet in the first age groups (0 to 2 years), and a relative specialization in the third age group. Environmental factors including sea surface temperature and chlorophyll-a concentrations were considered in order to explain differences in growth parameters and diet between different geographical areas. There was no significant relationship between the chlorophyll-a concentration and any growth parameter or L_{∞} . The only significant relationship observed with chlorophyll-a was with the anchovy at age⁻¹. Concerning temperature, there was significant relationship only between SST and the anchovy size at age⁻¹.

RÉSUMÉ. - Relations entre l'âge, la croissance, le régime alimentaire de l'anchois (*Engraulis encrasicolus* L.) et les paramètres de l'environnement de la baie de Bénisaf (SO Méditerranée, Ouest algérien).

L'âge, la croissance et le régime alimentaire de l'anchois ont été étudiés pour la première fois sur des échantillons provenant de la baie de Bénisaf (côte ouest algérienne), au cours de l'été (période de reproduction) et l'automne (période de recrutement) 2007. La structure d'âge et les paramètres de croissance ont été déterminés par lecture d'otolithes (sagitta). Le modèle de croissance de von Bertalanffy appliqué aux données âges-longueurs a montré que l'essentiel de la croissance de l'anchois est réalisé au cours de sa première année de vie. Ces résultats suggèrent que l'exploitation de ce stock dépend essentiellement des premiers groupes d'âges, lesquels dépendent fortement du succès du recrutement. La croissance des mâles et des femelles n'est pas significativement différente. Les paramètres de croissance des deux sexes confondus sont : $L_{\infty} = 15,61$ cm, $k = 0,75$ par an and $t_0 = -1,32$ ans. Quelle que soit la classe d'âge, l'anchois est strictement zooplanctonophage. Les copépodes constituent le groupe dominant (64% O ; 81% N), les autres crustacés, les larves de mollusques et les larves des poissons sont moins représentés. Les principales espèces de copépodes consommés sont par ordre d'importance: *Candacia longimana*, *Oncaea mediterranea* et *Pleuromamma abdominalis*. Les résultats indiquent que si le régime alimentaire des anchois est diversifié dans les premiers groupes d'âge (0 à 2 ans), il a tendance à se spécialiser à partir de trois ans. Des facteurs environnementaux comme la température de surface de la mer et la concentration en chlorophylle-a ont été examinés afin d'expliquer les différences de croissance et de régime alimentaire observées entre différentes zones géographiques. Il n'existe pas de relation significative entre la chlorophylle-a et les paramètres de croissance ou la longueur asymptotique (L_{∞}). La seule relation significative est observée entre la chlorophylle-a et la taille de l'anchois à l'âge⁻¹. Concernant la température, les seules relations significatives sont celles obtenues avec la taille de l'anchois à l'âge⁻¹.

Key words. - Engraulidae - *Engraulis encrasicolus* - MED - West Algeria - Anchovy - Growth - Age - Diet - Ontogenetic.

The European anchovy, *Engraulis encrasicolus* (Linné, 1758) is widely distributed in the Mediterranean Sea and constitutes one of the main fishing resources (Leonart and Maynou, 2002). This species is also an essential element of

(1) Université de Lille, FRANCE. [jean-michel.brylinski@univ-littoral.fr] [rachid.amara@univ-littoral.fr]

(2) ULCO, LOG, 62930 Wimereux, FRANCE.

(3) CNRS, UMR 8187, 62930 Wimereux, FRANCE. [Mahmoud.Bacha@univ-littoral.fr]

(4) Université de Bejaia, Laboratoire d'écologie et environnement, Targua ouzémour, 06000, Bejaia, ALGÉRIE.

(5) Université de Tlemcen, Faculté des sciences, Département de biologie, 13000 Tlemcen, ALGÉRIE. [econasro@gmail.com]

(6) IFREMER, Laboratoire ressources halieutiques, 150 quai Gambetta, BP 699, 62321 Boulogne-sur-Mer, FRANCE. [kelig.mahe@ifremer.fr]

* Corresponding author

marine food web due to its significant biomass at intermediate level (see Palomera *et al.*, 2007 for a review).

Most of the research on the ecology of this species was done in the north Mediterranean Sea (Tudela and Palomera, 1997; Morales-Nin and Perterra, 1990; Basilone *et al.*, 2004; Bellido *et al.*, 2000), the Black Sea and the Azov Sea (Mikhman and Tomanovich, 1977; Karacam and Duzgunes, 1990; Bulgakova, 1993), the Adriatic Sea (Dulčić, 1997; Coombs *et al.*, 2003) or the Bay of Biscay (Plounevez and Champalbert, 1999; Allain *et al.*, 2003; Díaz *et al.*, 2008, 2009).

As in the northern part of the Mediterranean Sea, anchovy and sardine, *Sardina pilchardus* (Walbaum, 1792), are the most important small pelagic fish in terms of biomass and commercial interest along the Algerian coast. In this area, the stock of pelagic fish was estimated by acoustic scientific surveys to be about 187 000 tons, and 60% of this stock was represented by anchovy (MPRH, 2004). Catches of the Algerian anchovy fishery exhibited great fluctuation during the past years, varying between 1374 and 6085 tons (Fish-Stat, FAO <http://faostat.fao.org/>). This species is considered as not over-exploited in Algerian waters (MPRH, 2004).

Despite the significant economic importance of this species along the North African Mediterranean coast, little information is known, either on its ecology or biology. Most studies are ancient and the only recent ones have been carried out in Tunisia and in Algeria (Arrignon, 1966; Quignard *et al.*, 1973; Gaamour *et al.*, 2004; Khemiri *et al.*, 2007; Bacha and Amara, 2009).

Populations of small pelagic fish, such as sardine and anchovy, show evidence of important natural fluctuations in their abundance (Lluch-Belda *et al.*, 1989; Martin *et al.*, 2008). These fluctuations seem to be related, among other factors, to climate variability (e.g., Sabatés *et al.*, 2007) or habitat conditions (Basilone *et al.*, 2004). Growth and feeding are two important parameters in fish population dynamics. Growth studies showed that anchovy has high growth rates and short life span (Basilone *et al.*, 2004; Khemiri *et al.*, 2007). Studies on the trophic ecology of anchovy have been performed to understand both the ecology of the species and the functioning of the pelagic ecosystem (Ré, 1996; Tudela and Palomera, 1997; Plounevez and Champalbert, 2000). In the Algerian coast, Bacha and Amara (2009) concluded that whatever the season, the region or the fish size, anchovy is exclusively zooplanktivorous and copepods were the most common prey. During its first year of life, anchovy feeds almost exclusively on copepods, and as anchovy grows, copepods are gradually substituted by large crustaceans. Temporal variability in satellite-derived chlorophyll-a matched the seasonal variability in the diversity of the anchovy preys and in the feeding intensity, as reflected by the vacuity index, suggesting further investigation of the potential use of satellite-derived chlorophyll-a data as

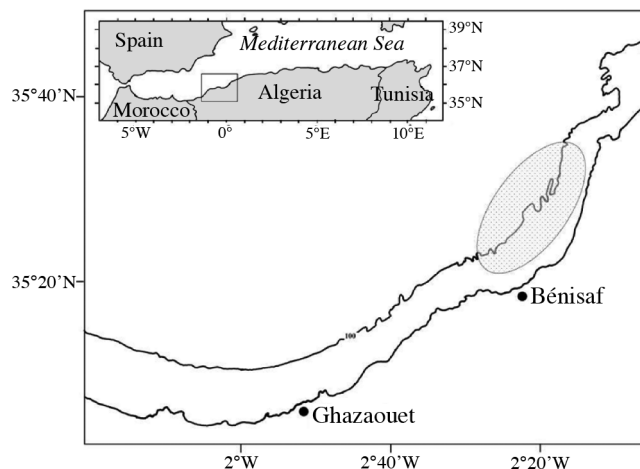


Figure 1. - Locations of sampling area in the Bay of Bénisaf (dotted area), Algerian coast, southwest Mediterranean Sea.

a proxy for anchovy feeding intensity. The close relationship between the environment and small pelagic population dynamics found in the study of Bacha and Amara (2009) evidences the need to increase the available data on growth and feeding in relation to environmental factors.

The southern part of the Mediterranean Sea (west Algerian coast) is a region clearly differentiated from the rest of the Mediterranean Basin by highly specific hydrological and ecological conditions (Millot, 1985). The aim of the present study is to describe the growth and diet of the European anchovy, and to test the influence of some environmental parameters (sea surface temperature and chlorophyll-a concentration) on the growth parameters.

MATERIALS AND METHODS

Study area and sampling

Samples of anchovy were collected monthly on board a commercial fishing vessel during the spawning and recruitment period between July and December 2007. Anchovy were caught by purse seine (mesh size of 8 mm) in the Bay of Bénisaf (from 35° 18'N and 1° 27'W to 35° 20'N and 1° 19'W, Fig. 1). In the laboratory, anchovy were measured (total length TL, cm) to the nearest 0.1 cm, sexed (when possible) and weighed (total weight W, g) with a precision of 0.1 g.

Age and growth estimation

Otoliths (sagittae) were taken through the gills as described in the method of Secor *et al.* (1992). After washing and cleaning, they were dried in the ambient air. The age reading and growth analysis were carried on 324 specimens: 137 males, 134 females and 53 undetermined sex specimens. To increase the evidence of the growth marks, otoliths were

covered with essential oil of cloves and then observed with a stereomicroscope under reflected light over a dark background. The alternating white and dark growth marks are called hyaline and opaque zones. The method used for reading and interpreting the age of anchovy followed those established and validated during the last workshop on anchovy otolith (Uriarte *et al.*, 2006). The birth date was established in summer time, on first of July; a date corresponding to the peak of the spawning period of anchovy in the Mediterranean Sea (Morales-Nin and Perterra, 1990; Khemiri *et al.*, 2007). The age of fish sampled before this date were assigned to the observed number of hyaline zones surrounded by opaque marks, whereas age of fish sampled during the second part of the year was established only by the number of hyaline zones. Each otolith was read twice, on two separate occasions, and readings for a given otolith were accepted only if both agreed. When there was a difference between the two readings, a third reading was performed and we considered the age value which was repeated twice. In this study, agreement between the two first readings was high and reached 90%.

Length-at-age data were fitted using the von Bertalanffy growth model:

$$L_t = L_{\infty} (1 - \exp(-k(t - t_0))),$$

where L_t is the expected length at age t years, L_{∞} is the asymptotic maximum length, k is the von Bertalanffy growth constant, and t_0 is the theoretical age at zero length. Growth curves were fitted for both males and females separately. The undetermined sex specimens were important to get a wider range of length for fitting the growth model and were included in both the male and female data sets. Estimation of growth parameters was done using Fishpar software (Prager *et al.*, 1987). Growth curves of males and females (without immature individuals) were compared using an analysis of covariance (ANCOVA). To compare the growth rate obtained in this study with those available for this species in other areas we calculated the growth performance index, $\Phi = \log_{10} k + 2 \log_{10} L_{\infty}$ (Pauly and Munro, 1984).

Stomach content analysis

After capture, stomachs were immediately preserved in 10% formalin following dissection of the fish. The stomachs were dissected later in the laboratory and vacuity index (V) was calculated as: $V = E/T \times 100$, where E was the number of empty stomachs and T the total number of stomachs analysed. The different preys ingested were sorted and identified to the lowest possible taxonomic group, using identification keys (Chevreux and Fage, 1925; Rose, 1933; Trégouboff and Rose, 1957; Conway *et al.*, 2003), counted and measured when possible. The size measurements were carried out on thirty individuals for each prey and average sizes were calculated.

Table I. - Von Bertalanffy growth parameters (L_{∞} , k and t_0) and the growth performance index (Φ) for males (M), females (F) and both sexes combined (M + F), (\pm standard deviation).

	L_{∞}	k	t_0	Φ (cm.y ⁻¹)
M+F	15.61 \pm 0.01	0.75 \pm 0.09	-1.32 \pm 0.08	2.26
F	15.76 \pm 0.01	0.79 \pm 0.12	-1.20 \pm 0.10	2.29
M	15.36 \pm 0.01	0.78 \pm 0.12	-1.28 \pm 0.10	2.26

Food composition was expressed as a percentage of frequency of occurrence (%O, the percentage of non-empty stomachs in which a certain prey item occurred) and percentage composition by number (%N, the number of a particular prey item as a proportion of the total number of all prey items in all stomachs). The diet diversity was expressed by the Shannon-Wiener diversity index (H') and the species richness (S). Furthermore, the Pielou's evenness index (J') was calculated to measure how evenly fish rely on food resources and the food niche width (B) in order to characterize the food resource spectrum used by anchovy. Factorial correspondence analysis (FCA) was performed using the matrix of frequency occurrence (%O) and percentage by number (%N) data to determine the pattern of prey distribution among age groups. Only prey items with occurrence >10% were used in the analyses.

Environmental variables

The following environmental variables have been considered in order to analyse the spatial anchovy growth parameters and diet variation: sea surface temperature (SST) and sea surface chlorophyll-a concentration (as an indicator of primary production, given that anchovy is a plankton feeder species). These data were derived from satellite imagery (<http://oceancolor.gsfc.nasa.gov>). Data used are average values over the year.

RESULTS

Age and growth

The anchovies analysed were composed of five age groups: 0, 1, 2, 3 and 4 years old and varied between 7 and 17 cm TL. Age groups 1 and 2 were the most abundant (36% and 24%), followed by age groups 0 (19%), 3 (15%) and 4 (6%). The estimation of growth parameters was carried out for each sex and for the two sexes combined (Tab. I and Fig. 2). An analysis of co-variance (ANCOVA) including the length (log-transformed) as a variable, the age as a co-variable and the sex as factor showed that there were no significant differences in growth patterns between males and females without considering the undetermined sex individuals ($F_{1,254} = 0.002$; $p = 0.959$). Pooled mean parameters were $L_{\infty} = 15.61$ cm, $k = 0.75$ per year and $t_0 = -1.32$ year.

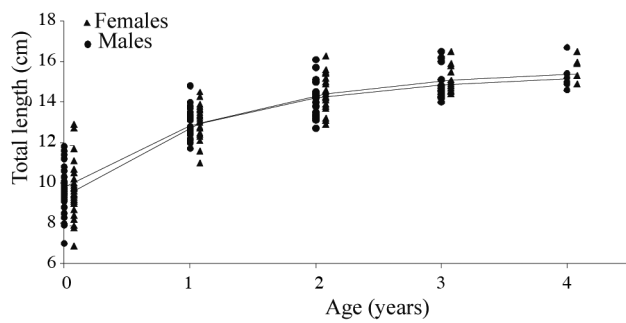


Figure 2. - Von Bertalanffy growth curves for males and females anchovy in the Bay of Bénisaf.

The growth performance index Φ was similar for both sexes (Tab. I).

The growth parameters and the size at age⁻¹ (L1) obtained from the literature for *E. encrasicolus* in different regions are shown in Table II together with the estimated mean chlorophyll-a concentrations and the annual mean SST for each area. Since growth parameters estimated by means of otolith interpretation differ from those estimated by scales or length frequency analyses, only the former one were reported in the present study. The relationships between the growth parameters for anchovy obtained from different regions with the mean SST and the mean chlorophyll-a concentration of the area are illustrated in figure 3. There was no significant relationship between the chlorophyll-a concentration and any growth parameter or L ∞ . These results were the same even when including the high chlorophyll-a value of the Azov Sea (14.94 mg.m⁻³) in the analysis. The only significant relationship observed with chlorophyll-a was with the anchovy at age⁻¹ ($r^2=0.36$; $F=5.754$; $p=0.037$).

Concerning temperature, there was significant relationship only between SST and the anchovy size at age⁻¹ ($r^2=0.33$; $F=5.395$; $p=0.04$) and Φ ($r^2=0.23$; $F=3.54$; $p=0.084$).

Diet composition

A total of 180 stomachs of anchovy, with a total length ranging from 7 to 16.2 cm (TL), was examined. Empty stomachs represented 12.7%. Thirty-three different prey were identified: 17 copepods, 4 amphipods, 5 decapods, 3 molluscs, and some other unidentified preys such as: mysids, euphausiids, ostracods and fish larvae (Tab. III). Copepods were the most important prey in all age groups, accounting for 81% by number of the prey taken and found in 64% of the anchovy examined. Three copepods species were particularly well represented in the diet: *Candacia longimana* (89% O; 39% N), *Oncaea mediterranea* (80% O; 8% N) and *Pleuromamma abdominalis* (73% O; 6% N). Brachyura (zoea), *Hyperia schizogeneios*, Brachyura (megalopa) and gastropods are also frequently preyed on by anchovy (respectively % O = 55%; 46.25%; 45%; 45%).

Ontogenetic changes in diet

The number and occurrence proportions of the major food categories varied with age (Tab. III). Crustaceans, mainly copepods dominated the diet of 0-group anchovy (< 11.8 cm TL). As anchovy grow, copepods are gradually substituted by larger prey such as decapods and amphipods.

The factorial correspondence analysis clearly illustrates the prey characteristics of each age group (Fig. 4). Axes 1 and 2 explain 87.15% of variance with 66.97% and 20.19% of inertia. Axis 1 separates the 0-group from the

Table II. - Growth parameters (k , y⁻¹ and Φ , cm.y⁻¹), asymptotic length (L ∞ , cm) and length at age⁻¹ (L1, cm) obtained for the anchovy *E. encrasicolus* in different regions. Mean annual \pm S.D. of chlorophyll-a concentration and sea surface temperature (SST). *: data from Basilone *et al.*, 2004.

Area	SST (°C)	Chlorophyll-a (mg.m ⁻³)	L ∞ (cm)	k (per year)	Φ : cm.y ⁻¹	Length at age ⁻¹	Source
West Algerian coast	19.44 \pm 0.10	0.33 \pm 0.06	15.61	0.75	2.267	12.87	This study
Algeria (Algiers)	19.24 \pm 3.81	0.35 \pm 0.90	16.57	0.59	2.205	11.87	Hémida (1987)
North Tunisian coast	21.15 \pm 0.05	0.22 \pm 0.02	19.16	0.32	2.028	12.90	Khemiri <i>et al.</i> (2007)
South Tunisian coast	21.89 \pm 0.06	0.45 \pm 0.25	17.19	0.36	2.069	10.35	Khemiri <i>et al.</i> (2007)
*Catalonian littoral (SE, Spain)	18.61 \pm 4.55	0.77 \pm 1.31	19.10	0.35	2.106	11.00	Morales-Nin and Perterra (1990)
*Gulf of Lion (SE, France)	16.72 \pm 3.60	1.23 \pm 1.61	19.10	0.35	2.106	11.00	Campillo (1992)
*Strait of Sicily	19.24 \pm 4.18	0.20 \pm 0.03	18.60	0.29	2.016	10.37	Basilone <i>et al.</i> (2004)
*Middle Ionian sea (Greece)	19.54 \pm 3.92	0.53 \pm 1.66	17.50	0.51	2.194	11.56	Machias <i>et al.</i> (2000)
*Middle-North Adriatic (Croatia)	17.57 \pm 4.27	0.28 \pm 0.16	19.40	0.57	2.331	11.15	Sinovic (2000)
*North Portugal	15.95 \pm 1.89	2.24 \pm 1.46	15.80	0.53	2.120	-	Ramos and Santos (1999)
Black Sea	18.89 \pm 0.05	0.77 \pm 0.04	16.76	0.32	1.960	10.48	Erkoyuncu and Ozdamar (1989)
Azov Sea	18.19 \pm 0.05	14.94 \pm 0.43	13.30	0.61	2.030	10.89	Volovik and Kozlitina (1983)
Bay of Biscay	15.95 \pm 3.48	1.22 \pm 1.92	22.10	0.57	2.446	9.85	Guérault and Avrilla (1974)
*Cantabrian Sea, N Spain	15.95 \pm 3.48	1.22 \pm 1.92	21.30	0.48	2.343	9.60	Cendrero <i>et al.</i> (1981)

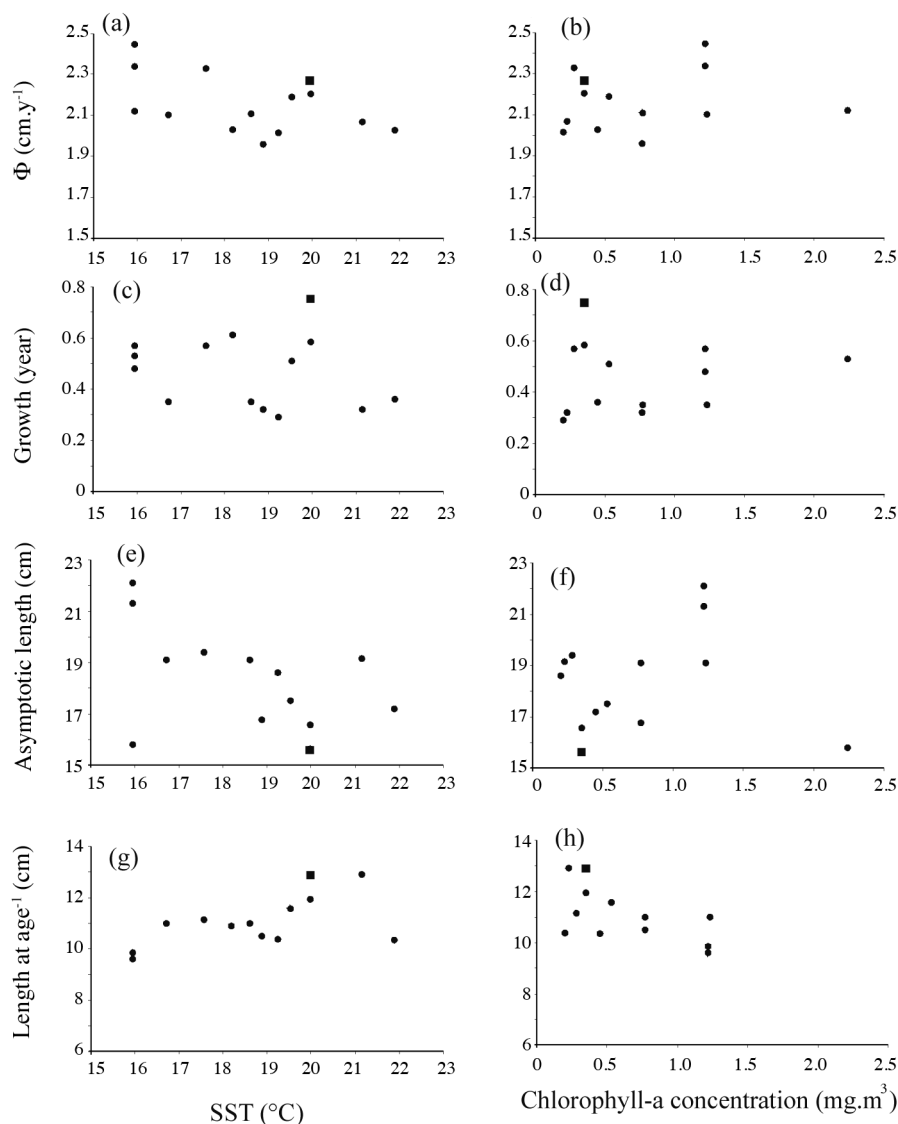


Figure 3. - Relationships between mean sea surface temperature (SST, °C) and chlorophyll-*a* concentrations with the growth performance index Φ (a, b), body growth coefficient k (c, d), asymptotic length L_{∞} (e, f) and length at age⁻¹ (g, h). (● Data from table II; ■ Data from present study).

others, showing a gradient in length of prey. Indeed, large prey and small prey have positive and negative values (of factorial coordinates), respectively, along the first axis. The copepods (*Centropages chierchiae*, *Temora stylifera*) have a high positive value and the fish larvae a high negative value. The 0-group situated in the positive part of axes 1 and 2 is associated with the dominance and high occurrence of small and medium copepods, such as *Corycaeus* sp., *Scolecithrix brady*, *C. chierchiae*, *Oncaea venusta*, *Sapphirina metallina*, *T. stylifera* and *Aetideus armatus*. The groups (1 and 2) presented in the negative part of axes 1 and 2 are more diversified and linked with the occurrence of medium and large prey (copepods, decapods, amphipods and gastropods). Finally, the group 3+ located in the positive part of axis 2 and negative part of axis 1 is discriminated by the occurrence of very

large prey such as euphausiids, brachyura (zoea and megalops), fish larvae, mysids and finally the very large copepods (*Euchirella messinensis* and *Arietellus setosus*).

Species richness (S), Shannon-Weiner diversity (H'), Pielou's evenness (J) and food niche width (B) varied between age groups (Tab. III). The diversity index and the food niche width increased from 0-group to group 2 (respectively: from 2.16 to 2.22 and 8.67 to 9.21) and declined in group 3+ (respectively: 1.91 and 6.75). Pielou index (J) showed highest values in group 2 (0.74) and the lowest in group 3+ (0.56). This tendency in the lower indices in the age group 3+ indicates a diversification of the feeding in the first age group (0 to 2 years), and a relative specialization in the third age group. Vacuity index increased from the age 0 to age 2 and tended to zero in age group 3+.

Table III. - Occurrence (% O) and percentage number (% N) of prey found in stomachs of anchovy in the Bay of Bénisaf. Species richness, Shannon-Wiener, Pielou's evenness, food niche width and vacuity index for each age group are listed below the table.

			G0		G1		G2		G3+	
			O%	N%	O%	N%	O%	N%	O%	N%
Ostracoda	Unidentified Ostracoda	(Ostr)	23.81	0.22	16.13	0.41	17.65	0.53	7.69	0.29
	<i>Aetideus armatus</i>	(Aarm)	23.81	0.44	12.90	0.29	5.88	0.13	15.38	0.43
Copepoda	<i>Arietellus setosus</i>	(Aset)	4.76	0.19	3.23	0.17	5.88	0.26	23.08	0.43
	<i>Candacia longimana</i>	(Clon)	95.24	28.29	80.65	47.07	82.35	32.70	100	54.65
	<i>Calocalanus</i> sp.		4.76	0.12	-	-	-	-	-	-
	<i>Centropages chierchiae</i>	(Cchi)	80.95	8.03	6.45	0.35	-	-	7.69	0.14
	<i>Corycaeus</i> sp.	(Cory)	57.14	1.21	12.90	0.41	11.76	0.26	7.69	0.43
	<i>Euchirella messinensis</i>	(Emes)	-	-	3.23	0.17	-	-	23.08	2.32
	<i>Lubbockia aculeata</i>	(Lacu)	-	-	-	-	-	-	7.69	0.14
	<i>Microsetella rosea</i>	(Mros)	28.57	0.44	16.13	0.65	52.94	4.29	38.46	1.01
	<i>Oncaea mediterranea</i>	(Omed)	95.24	11.54	74.19	6.27	94.12	12.46	53.85	3.05
	<i>Oncaea venusta</i>	(Oven)	47.62	0.60	16.13	0.77	-	-	23.08	1.01
	<i>Pleuromamma abdominalis</i>	(Pabd)	80.95	4.14	67.74	3.64	64.71	11.12	76.92	7.55
	<i>Sapphirina metallina</i>	(Smet)	66.67	1.97	16.13	2.15	11.76	5.22	30.77	0.87
	<i>Scolecithrix brady</i>	(Sbra)	61.90	2.20	16.13	0.59	-	-	15.38	0.29
	<i>Scolecithrix danae</i>	(Sdan)	76.19	4.81	32.26	3.40	17.65	0.53	23.08	0.58
	<i>Temora stylifera</i>	(Tsty)	85.71	21.30	12.90	3.10	-	-	7.69	0.14
	Unidentified Copepoda	(Ucop)	90.48	11.00	67.74	5.43	64.71	9.78	61.54	4.36
Mysida	Unidentified Mysida	(Mysi)	-	-	-	-	-	-	7.69	0.43
Amphipoda	<i>Primno macropa</i>	(Pmac)	-	-	12.90	0.47	5.88	0.40	7.69	0.14
	<i>Lestrigonus schizogeneios</i>	(Lsch)	28.57	0.28	61.29	2.68	35.29	1.20	46.15	1.74
	<i>Phrosina semilunata</i>	(Psem)	4.76	0.09	48.39	5.31	35.29	4.96	61.54	6.83
	Unidentified Amphipoda	(Uamp)	9.52	0.06	25.81	1.73	17.65	0.53	23.08	0.58
Euphausiacea	Unidentified Euphausiacea	(Euph)	9.52	0.25	22.58	2.74	5.88	0.80	15.38	0.29
Decapoda	<i>Brachyura</i> (Zoea)	(Bzoe)	57.14	1.08	70.97	3.46	23.53	4.42	46.15	2.32
	<i>Brachyura</i> (Metazoea)	(Bmet)	-	-	3.23	0.06	-	-	7.69	0.43
	<i>Brachyura</i> (Megalopa)	(Bmeg)	19.05	0.22	61.29	4.18	29.41	6.43	61.54	5.81
	<i>Solenocera membranacea</i>	(Smem)	4.76	0.09	6.45	0.11	-	-	-	-
	Decapoda larvae	(Deca)	4.76	0.06	22.58	2.38	17.65	0.40	7.69	0.29
Mollusca	Unidentified Bivalvia	(Biva)	4.76	0.03	3.23	0.06	-	-	7.69	0.29
	Unidentified Gasteropoda	(Gast)	57.14	1.21	25.81	1.67	64.71	3.48	46.15	2.76
	Cephalopoda larvae	(Ceph)	-	-	3.23	0.11	-	-	-	-
Vertebrata	Unidentified fish larvae	(Fish)	-	-	-	-	-	-	15.38	0.29
Species richness			26		29		20		30	
Shannon-Wiener index			2.16		2.19		2.22		1.91	
Pielou's evenness index			0.66		0.65		0.74		0.56	
Food niche width			8.67		8.94		9.21		6.75	
Vacuity index (%)			4		16		21		0	

DISCUSSION

Anchovy is a small pelagic fish with fast growing but it is also a short-lived species (Pauly, 1982). Our sampling

suggested that the life expectancy of the anchovy in the Bay of Bénisaf reaches 4 years. This longevity corresponds to the lifespan reported for this species in the Tunisian waters (Khemeri *et al.*, 2007), the Adriatic Sea (Sinovcic, 2000)

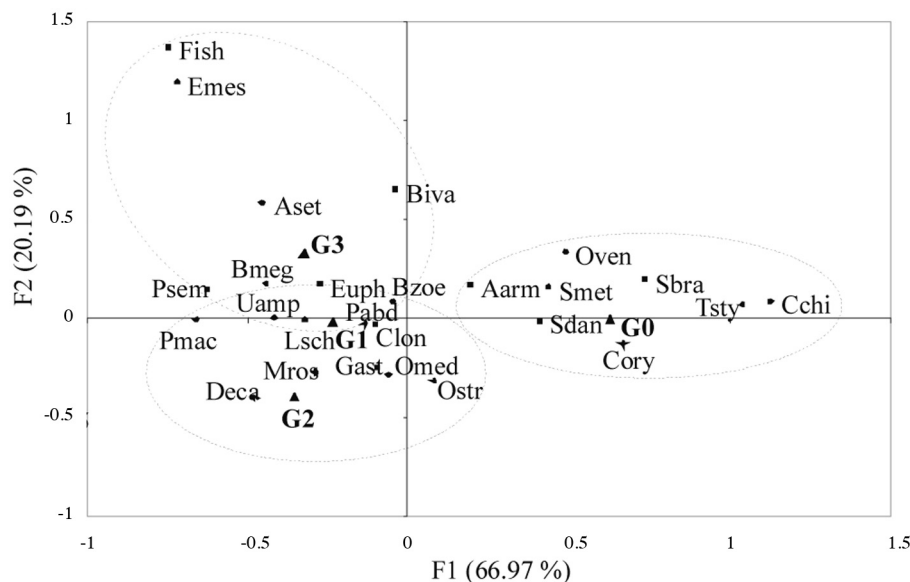


Figure 4. - Factorial correspondence analysis for prey and age groups in the Bay of Bénisaf (FCA based on frequency of prey occurrence): See table III for an explanation of the codes used. Prey specific to each age group are surrounded by dotted lines.

and the Northwestern Mediterranean Sea (Morales-Nin and Perterra, 1990). Just like many pelagic species, a very small fraction of the population usually reaches ages four and five (Bailey, 1992).

The von Bertalanffy growth function fitted to age-length data showed that most of the growth of the anchovy is achieved during the first year of life. Length at one-year old was estimated to be 12.87 cm suggesting that this stock is primarily supported by the smallest age groups (0 and 1-group), thus showing a strong dependence on recruitment success. These results are in agreement with those obtained in the Gulf of Cadiz (SW Spain) by Bellido *et al.* (2000). This latter showed that anchovy reaches 60% of its asymptotic length in its first year of life and 83% in its second. Our results suggests that the west coast Algerian anchovy grow more rapidly during the first year of life and attain a smaller asymptotic length than their conspecific at higher latitude (e.g., Bay of Biscay). Environmental factors such as sea temperature and chlorophyll-a concentration seem to affect the size attained at the end of the first year of life. We found significant relationships between the anchovy size at age⁻¹ and SST or chlorophyll-a concentration in the different areas.

After the first year, the annual growth rate drops rapidly and this is probably related to sexual maturity since individuals are generally mature by the first year of life in the studied area. In the northern part of the Mediterranean Sea, anchovy reaches first maturity at 11 cm in the Alboran Sea (Giraldez and Abad, 1995). This size is lower in the southern part of Mediterranean Sea (7.3 cm along the Tunisian coast, Gaamour *et al.*, 2004). The first maturity in the Bay of Algiers is reached at about 11 cm for both sexes (Djabali *et al.*, 1988; Hemida, 1987). These values are higher than those reported by Bacha *et al.* (unpubl. data) in the Gulf of Bejaia

(9 cm for both sexes). Hence, from the end of the first year of life, energy is supposed to be allocated to reproduction, with less energy available for somatic growth.

Population of anchovy occurs at different latitudes and inhabits environments that differ in both mean annual temperature and length of the growing season. In the Bay of Bénisaf, anchovy seems to have higher growth parameters most likely in relation with environmental variables. Indeed, the west Algerian coast is a region clearly differentiated from the rest of the Mediterranean Basin by highly specific hydrological and ecological conditions (Millot, 1985). The extreme western Algerian coast is constantly influenced by the cold plankton-rich currents from the Atlantic entering the Mediterranean through the Strait of Gibraltar, which extends eastwards (Benzohra and Millot, 1995). This richness is reflected by the higher anchovy prey diversity and a lower stomach vacuity index in the western Algerian coast compared to the eastern one (Bacha and Amara, 2009). The estimated growth parameter *k* of the Bay of Bénisaf anchovy was at the top of the range observed for this fish species in different areas (Tab. II). The estimated length at age⁻¹ in this study (12.87 cm) was comparable to the one estimated for the Tunisian coast (Khemiri *et al.*, 2007) but slightly higher than that observed in the northern part of the Mediterranean Sea or the Bay of Biscay. The growth performance index obtained for the anchovy of the Bay of Bénisaf (2.26) was very similar to that estimated in other areas of the Mediterranean Sea (Tab. II) suggesting that anchovy has similar growth patterns in this area. The impact of temperature on metabolic rates and thereby on growth has been demonstrated for adult fishes (Pauly 1980). Fish tend to have lower asymptotic length with increasing temperature. Compared to the Mediterranean Sea, the Bay of Biscay anchovy seems

to attain higher asymptotic length. The Mediterranean Sea is characterized by higher temperatures, compared to the Bay of Biscay, and the variation ranges in temperature are very low (Basilone *et al.*, 2004). This may explain the very close values of the growth rates obtained for anchovy in the Mediterranean Sea.

Contrary to the study of Basilone *et al.* (2004) no clear relationship between sea surface chlorophyll-a concentration and growth parameters or L_{∞} were observed. Sea surface estimates of chlorophyll concentrations were reported to be good indicators of food availability for anchovy (Bacha and Amara, 2009). Phytoplankton is consumed by zooplankton, which is the main food item for many fish larvae of many species, and for small pelagic fish such as anchovy. In the Strait of Sicily and in the Catalan sea, a good correspondence between anchovy growth and chlorophyll concentration has been showed (Basilone *et al.*, 2004; Martin *et al.*, 2008). Although the chlorophyll-a concentration along the Algerian coast was low, the growth parameters and the size at age⁻¹ of the anchovy along the Algerian coast were higher than in other areas indicating that the anchovy growth in this area was not limited by the food. However the existence of several genetically distinct populations of anchovy in the Mediterranean Sea (north and south) (Kristoffersen and Magoulas, 2008) may partly explain variations in growth parameters in different populations and lead us to suggest norms of reaction (growth, size and age at maturity) to the various SST and/or chlorophyll-a for each population. Indeed, Fage (1920) suggested that differences in growth, and some morphometric characteristics, allowed to distinguish two races of European anchovies, an Atlantic and Mediterranean one. Recently, two anchovy species were identified: *Engraulis albidus* sp. and *Engraulis encrasicolus* with differences in their growth rate and maximal length. (Bembo *et al.*, 1996; Borsa *et al.*, 2004).

Trophic ecology studies of adult anchovy carried out in NW Mediterranean Sea emphasize that this species feeds on small zooplankton, mostly copepods, and to a lesser extent on molluscs, cladocerans, other crustaceans and appendicularians (Tudela and Palomera, 1995; 1997; Plounevez and Champalbert, 2000). In the Bay of Bénisaf, we found that anchovy fed exclusively on zooplankton, the main prey items being copepods, and to a lesser extent on amphipods, decapods and molluscs. Other large prey like crustacean larvae (euphausiids and mysids) and fish larvae sporadically occurred in the diet. Three copepods were particularly well represented in the diet of anchovy in the Bay of Bénisaf: *Candacia longimana*, *Oncaea mediterranea* and *Pleuromamma abdominalis*. Although anchovy feeds preferentially on copepods, prey species differ according to geographical areas. Tudela and Palomera (1995, 1997) found that the main prey species for anchovy in the northwest Mediterranean Sea were *Centropages typicus*, *Temora stylifera*, *Micro-*

setella rosea and *Oncaea* spp. In the Gulf of Lions, adult anchovy feed mainly on *Candacia armata*, *Microsetella rosea*, Clausocalanidae-Paracalanidae and *Temora stylifera* (Plounevez and Champalbert, 2000). *Temora longicornis*, *Oncaea* sp., *Corycaeus* sp. and *Centropages chierchiae* are the dominant prey of anchovy in the Bay of Biscay (Plounevez and Champalbert, 2000). Most published literature also reported that larger prey sporadically occurred in the diet of anchovy. These were mainly captured at night and depended primarily on fish size and age (Tudela and Palomera, 1995; Plounevez and Champalbert, 1999). Spatial differences in prey species may be attributable to differences in prey availability in response to the existence of differing hydrographic structures in the respective distribution areas considered (Riandey *et al.*, 2005).

On the other hand, an ontogenetic shift in diet was observed. This study showed that during the first year of life, anchovy feeds almost exclusively on copepods (mainly small and medium size prey). As anchovy grows, copepods are gradually substituted by large crustaceans such as decapods and amphipods and they become more frequent in the diet of age groups 1, 2 and 3+. These results agree with reports on fish in general and on anchovy in particular. Indeed several authors have demonstrated that many fish species exhibit substantial ontogenetic changes in taxonomic composition and size range of prey consumed (e.g., Plounevez and Champalbert, 1999; Mahé *et al.*, 2007). These shifts have been attributed to habitat or behavioural changes related to increasing body size or age of the predator (Grossman, 1980; Schmitt and Holbrook, 1984). Changes associated with increased body size, such as increased swimming speed and maximum gap size, may substantially increase the suite of prey available to a predator as it grows (Ross, 1978; Stoner, 1980). Visual acuity and reaction distance to prey also increase with increasing predator size (Breck and Gitter, 1983). As demonstrated by Bulgakova (1996) for adult anchovy, the size range of prey increases with increasing fish size range. On the other hand, the occurrence and weight of the small-sized copepods decreased with increasing fish length (Plounevez and Champalbert, 2000; present study). The gradual emergence of large copepods and large crustaceans in the age groups 1 to 3+ indicated selectivity for larger prey with higher energy and could be associated with sexual maturity of anchovy, at the end of the first year of life. This may be explained by the energy needed by anchovy to accomplish its reproduction. As hypothesised for the temperate herring *Clupea harengus*, individuals maximize their dietary intake and spawning capacity by feeding selectively on large, high-energy prey (Rajasilta, 1992).

CONCLUSIONS

Anchovy represents a fundamental link between plankton production and predators of upper trophic levels. All the studies conducted on anchovy (larval, juvenile and adult stages) confirm the important role played by copepods as the major link between phytoplankton and anchovy production (Tudela and Palomera, 1995; Plounevez and Champalbert, 2000, present study). Although overfishing has played a role in many of the major declines of small pelagic stocks, environmental variability is also thought to be a key contributor to this extreme population variability (e.g., Cury *et al.*, 2000). The influence of sea surface temperature and chlorophyll-a concentration on the growth of anchovy during its first year of life has been highlighted in the present study. Anchovy populations in the Algerian coast are supported mainly by the smallest age groups and have therefore a strong dependence on recruitment success. Their life history traits (high mobility, zooplankton feeders and short life span) make them particularly sensitive to environmental changes. The close relationship between the environment and anchovy population dynamics (Conway *et al.*, 1998; Martin *et al.*, 2008) emphasizes the need to increase the understanding on the growth and feeding behaviour of this species in relation to plankton dynamics and other environmental factors.

REFERENCES

- ALLAIN G., PETITGAS P., GRELLIER P. & LAZURE P., 2003. - The selection process from larval to juvenile stages of anchovy (*Engraulis encrasicolus*) in the Bay of Biscay investigated by Lagrangian simulations and comparative otolith growth. *Fish. Oceanogr.*, 12: 407-418.
- ARRIGNON J., 1966. - L'anchois (*Engraulis encrasicolus*) des côtes d'Oranie. *Rev. Trav. Inst. Pêch. Marit.*, 30(4): 317-342.
- BACHA M. & AMARA R., 2009. - Spatial, temporal and ontogenetic variation in diet of anchovy (*Engraulis encrasicolus*) on the Algerian coast (SW Mediterranean). *Estuarine, Coastal Shelf Sci.*, 85: 257-264.
- BAILEY R.S., 1992. - The global pelagic fish resources and its biological potential. In: *Pelagic Fish: The Resource and its Exploitation* (Burt J.R., Hardy R. & Whittle K.J., eds), pp. 1-20. Cambridge: Cambridge Univ. Press.
- BASILONE G., GUISANDE C., PATTI B., MAZZOLA S., CUTTITTA A., BONANNO A. & KALLIANIOTIS A., 2004. - Linking habitat conditions and growth in the European anchovy (*Engraulis encrasicolus*). *Fish. Res.*, 68: 9-19.
- BELLIDO J.M., PIERCE G.J., ROMERO J.L. & MILLAN M., 2000. - Use of frequency analysis methods to estimate growth of anchovy (*Engraulis encrasicolus* L. 1758) in the Gulf of Cadiz (SW Spain). *Fish. Res.*, 48: 107-115.
- BEMBO D.G., CARVALHO G.R., CINGOLANI N. & PITCHER T.J., 1996. - Stock discrimination among European anchovies, *Engraulis encrasicolus*, by the means of PCR-amplified mitochondrial DNA analysis. *Fish. Bull.*, 94: 31-40.
- BENZOHRA M. & MILLOT C., 1995. - Characteristics and circulation of the surface and intermediate water masses off Algeria. *Deep-Sea Res.*, 42(10): 1803-1830.
- BORSA P., COLLET A. & DURAND J.D., 2004. - Nuclear-DNA markers confirm the presence of two anchovy species in the Mediterranean. *C. R. Biol.*, 327: 1113-1123.
- BRECK J.E. & GITTER M.J., 1983. - Effect of fish size on the reactive distance of bluegill (*Lepomis macrochirus*) sunfish. *Can. J. Fish. Aquat. Sci.*, 40: 162-167.
- BULGAKOVA Y.U., 1993. - Daily feeding dynamics of the Black Sea anchovy, *Engraulis encrasicolus*. *J. Ichthyol.*, 33: 78-88.
- BULGAKOVA Y.U., 1996. - Feeding in the Black sea anchovy: diet composition, feeding behaviour, feeding periodicity and daily rations. *Sci. Mar.*, 60(2): 283-284.
- CAMPILLO A., 1992. - Les pêcheries françaises de Méditerranée : synthèse des connaissances. 206 p. Rapport interne Ifremer/RV N° 92/019-RH Sète.
- CENDRERO O., CORT J.L. & DE CARDENAS E., 1981. - Revisión de algunos datos sobre la biología de la anchoa, *Engraulis encrasicolus* (L.) del Mar Cantábrico. *Bol. Inst. Esp. Oceanogr.*, 6: 117-124.
- CHEVREUX E. & FAGE L., 1925. - Amphipodes. In: *Faune de France*, 9: 1-488.
- CONWAY D.V.P., COOMBS S.H. & SMITH C., 1998. - Feeding of anchovy *Engraulis encrasicolus* larvae in the North Western Adriatic Sea in response to changing hydrobiological conditions. *Mar. Ecol. Prog. Ser.*, 175: 35-49.
- CONWAY D., WHITE R.G., HUGUES-DIT-CILES J., GALLIENNE C.P. & ROBINS D.B., 2003. - Guide to the Coastal and Surface Zooplankton of the South-Western Indian Ocean. 356 p. Plymouth, UK: Occasional Publication of the Marine Biological Association of the United Kingdom, No. 15.
- COOMBS S.H., GIOVANARDI O. & HALLIDAY N.C., 2003. - Wind mixing, food availability and mortality of anchovy larvae *Engraulis encrasicolus* in the Northern Adriatic Sea. *Mar. Ecol. Prog. Ser.*, 248: 221-235.
- CURY P., BAKUN A., CRAWFORD R.J.M., JARRE A., QUIÑONES R.A., SHANNON L.J.H. & VERHEYE M., 2000. - Small pelagic in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES J. Mar. Sci.*, 57: 603-618.
- DÍAZ E., TXURRUKA J.M. & VILLATE F., 2008. - Biochemical composition and condition in anchovy larvae *Engraulis encrasicolus* during growth. *Mar. Ecol. Prog. Ser.*, 361: 227-238.
- DÍAZ E., TXURRUKA J.M. & VILLATE F., 2009. - Biochemical composition and somatic growth of pelagic larvae of three fish species from the Bay of Biscay. *Mar. Ecol. Prog. Ser.*, 382: 173-183.
- DJABALI I., MOULOUD F. & HEMIDA F., 1988. - Résultats des travaux réalisés sur les stocks de sardines et des anchois des côtes algéroises. *FAO Rapp. Pêches*, 395: 112-120.
- DULČIĆ J., 1997. - Growth of anchovy, *Engraulis encrasicolus* (L.), larvae in the Northern Adriatic Sea. *Fish. Res.*, 31: 189-195.
- ERKOYUNCU I. & OZDAMAR E., 1989. - Estimation of the age, size and sex composition and growth parameters of anchovy, *Engraulis encrasicolus* (L.) in the Black Sea. *Fish. Res.*, 7: 241-247.
- FAGE L., 1920. - Engraulidae, Clupeidae. *Rep. Danish Oceanog. Exp. Medit.*, 2(A9): 1-136.
- GAAMOUR A., KHEMIRI S., MILI S. & BEN ABDALLAH L., 2004. - L'anchois (*Engraulis encrasicolus*) des côtes nord de la Tunisie : reproduction et exploitation. *Bull. Inst. Natl. Sci. Tech. Mer Salammbô*, 31: 17-24.

- GIRALDEZ A. & ABAD R., 1995. - Aspects on the reproductive biology of the Western Mediterranean anchovy from the coasts of Málaga (Alborán Sea). *Sci. Mar.*, 59(1): 15-23.
- GROSSMAN G.D., 1980. - Ecological aspects of ontogenetic shifts in prey size utilisation in the bay goby (Pisces: gobiidae). *Oecologia*, 47: 233-238.
- GUÉRAULT D. & AVRILLA J.L., 1974. - L'anchois du golfe de Gascogne : taille, âge, croissance. *Cons. Int. Explor. Mer*, C.M. 1974/J: 17.
- HEMIDA F., 1987. - Contribution à l'étude de l'anchois *Engraulis encrasicolus* (Linné, 1758) dans la région d'Alger : biologie et exploitation. Thèse de Magister, 136 p. USTHB, Alger.
- KARACAM H. & DUZGUNES E., 1990. - Age, growth and meat yield of the European anchovy (*Engraulis encrasicolus*, L. 1758) in the Black Sea. *Fish. Res.*, 9: 181-186.
- KHEMIRI S., GAAMOUR A., MEUNIER F. & ZYLBERBERG I., 2007. - Age and growth of *Engraulis encrasicolus* (Clupeiformes: Engraulidae) in the Tunisian waters. *Cah. Biol. Mar.*, 48: 259-269.
- KRISTOFFERSEN J.B. & MAGOULAS A., 2008. - Population structure of anchovy *Engraulis encrasicolus* L. in the Mediterranean Sea inferred from multiples methods. *Fish. Res.*, 91: 187-195.
- LLEONART J. & MAYNOU F., 2002. - Fish stock assessments in the Mediterranean: state of the art. *Sci. Mar.*, 67(1): 37-49.
- LLUCH-BELDAD., CRAWFORD R.J.M., KAWASAKI T., MACCALL A.D., PARRISH R.H., SCHWARTZLOSE R.A. & SMITH P.E., 1989. - World-wide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. Mar. Sci.*, 8: 195-205.
- MACHIAS A., SOMARAKIS S., KAPADAGAKIS P., DRAKOPOULUS P., GIANNOULAKI M., MARAVEYA E., MANOUSAKIS L., VATSOS D., TSIMENIDOU C. & TSIMENIDES N., 2000. - Evaluation of the southern Greek anchovy stocks. Final report DGXIV contract no. 97/0048.
- MAHÉ K., AMARA R., BRYCKAERT T., KACHER M & BRYLINSKI J.M., 2007. - Ontogenetic and spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and the Celtic Sea. *ICES. J. Mar. Sci.*, 64: 1210-1219.
- MARTIN P., BAHAMON N., SABATES A., MAYNOU F., SANCHEZ P. & DEMESTRE M., 2008. - European anchovy (*Engraulis encrasicolus*) landings and environmental conditions on the Catalan Coast (NW Mediterranean) during 2000-2005. *Hydrobiologia*, 162: 185-199.
- MIKHMAN A.S. & TOMANOVICH L.V., 1977. - The feeding of the Azov anchovy, *Engraulis encrasicolus maeoticus*. *J. Ichthyol.*, 17: 240-244.
- MILLOT C., 1985. - Some features of the Algerian current. *J. Geophys. Res.*, 90: 7169-7176.
- MORALES-NIN B. & PERTIERRA J.P., 1990. - Growth rates of the anchovy *Engraulis encrasicolus* and the sardine *Sardina pilchardus* in the Northwestern Mediterranean Sea. *Mar. Biol.*, 107: 349-356.
- MPRH, 2004. - Plan national de développement de la pêche et de l'aquaculture 2003-2007. 77 p. Rapport du ministère de la Pêche et des Ressources halieutiques, Algérie.
- PALOMERA I., OLIVAR M.P. & SALAT J., 2007. - Small pelagic fish in the NW Mediterranean Sea: an ecological review. *Prog. Oceanogr.*, 74: 377-396.
- PAULY D., 1980. - On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. Int. Explor. Mer.*, 39: 175-192.
- PAULY D., 1982. - Studying single-species dynamics in a multi-species context. In: Theory and Management of Tropical Fisheries. ICLARM Conf. Proc. 9 (Pauly D. & Murphy G.I., eds), pp. 33-70. Manila: International Centre for Living Aquatic Resource Management.
- PAULY D. & MUNRO J.L., 1984. - Once more on the comparison of growth in fish and invertebrates. *ICLARM Fishbyte*, 2(1): 21.
- PLOUNEVES S. & CHAMPALBERT G., 1999. - Feeding Behaviour and Trophic Environment of *Engraulis encrasicolus* (L.) in the Bay of Biscay. *Estuarine Coastal Shelf Sci.*, 49: 177-191.
- PLOUNEVES S. & G. CHAMPALBERT, 2000. - Diet, feeding behaviour and trophic activity of the anchovy (*Engraulis encrasicolus* L.) in the Gulf of Lion (Mediterranean Sea). *Oceanol. Acta*, 23: 175-192.
- PRAGER M.H., SAILA S.B. & RECKSIEK C.W., 1987. - Fishparm a microcomputer Program for parameter estimation of nonlinear models in fishery science. *Old Dom. Univ. Res. Found., Tech. Rep.*, 87-10: 1-37.
- QUIGNARD J.P., HAMDOUNI T. & ZAOUALI J., 1973. - Données préliminaires sur les caractères biométriques des anchois *Engraulis encrasicolus* (Linné, 1758) des côtes de Tunisie et du lac Ichkeul. *Rev. Trav. Inst. Pêch. Mar.*, 37: 191-196.
- RAJASILTA M., 1992. - Relationship between food, fat, sexual maturation, and spawning time of Baltic herring (*Clupea harengus membras*) in the Archipelago Sea. *Can. J. Fish. Aquat. Sci.*, 49: 644-65.
- RAMOS S. & SANTOS P., 1999. - Crescimento do biqueirao (*Engraulis encrasicolus* Linnaeus, 1758) na costa norte de Portugal. *Rev. Biol.*, 17: 211-216.
- RÉ P., 1996. - Anchovy spawning in the Mira estuary (southwestern Portugal). *Sci. Mar.*, 60(2): 141-153.
- RIANDEY V., CHAMPALBERT G., CARLOTTI F., TAUPIER-LETAGE I. & THIBAUT-BOTHA D., 2005. - Zooplankton distribution related to the hydrodynamic features in the Algerian Basin (western Mediterranean Sea) in summer 1997. *Deep-Sea Res.*, 52: 2029-2048.
- ROSE M., 1933. - Les copépodes pélagiques. In: Faune de France, 26: 1-374.
- ROSS S.T., 1978. - Trophic Ontogeny of the leopard searobin, *Prionotus scitulus* (Pisces: Triglidae). *US Fish. Bull.*, 76: 225-234.
- SABATÈS A., OLIVAR M.P., SALAT J., PALOMERA I. & ALEMANY F., 2007. - Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Prog. Oceanogr.*, 74: 355-376.
- SECOR D.H., 1992. - Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass *Morone saxatilis*. *Fish. Bull.*, 90: 798-806.
- SCHMITT R.J. & HOLBROOK S.J., 1984. - Gape-limitation, foraging tactics and prey size selectivity of two microcarnivorous species of fish. *Oecologia*, 63: 6-12.
- SINOVCIC G., 2000. - Anchovy, *Engraulis encrasicolus* (Linnaeus, 1758): biology, population dynamics and fisheries case study. *Acta Adriat.*, 41: 3-53.
- STONER A.W., 1980. - Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): variation and functional responses. *US Fish. Bull.*, 78: 337-352.

- TRÉGOUBOFF G. & ROSE M., 1957. - Manuel de Planctonologie méditerranéenne. Vol. I (texte, 587 p.) et Vol. II (illustrations, 207 p.). Paris: CNRS.
- TUDELA S. & PALOMERA I., 1995. - Diel feeding intensity and daily ration in the anchovy *Engraulis encrasicolus* in the Northwest Mediterranean Sea during the spawning period. *Mar. Ecol. Prog. Ser.*, 129: 55-61.
- TUDELA S. & PALOMERA I., 1997. - Trophic ecology of the European anchovy *Engraulis encrasicolus* in the Catalan Sea (Northwest Mediterranean). *Mar. Ecol. Prog. Ser.*, 160: 121-134.
- URIARTE A., DUEÑAS C., DUHAMEL E., GRELLIER P., RICO I. & VILLAMOR B., 2006. - Anchovy Otolith Workshop, Working Document to the 2007 ICES Planning Group on Commercial Catch, Discards and Biological Sampling (PGCCDBS) (5-9 March). In: AZTI, Pasaia, Basque Country, Spain, 58 p.
- VOLOVIK S.P. & KOZLITINA S.V., 1983. - Assessment of the potential catch of the Azov anchovy, *Engraulis encrasicolus* (Engraulidae), in relation to growth and structure of its population. *J. Ichthyol.*, 23: 26-38.